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THE RELATIONS OF THE ANTERIOR VISCERAL ARCHES TO THE CHONDROCRANIUM.

W. K. GREGORY.

The articular relations with the chondrocranium of the upper and lower jaw-cartilages and the hyomandibular, as typified in *Ceratodus*, in *Squalus*, and in *Notidanus*, are in themselves of course generally understood, but comparison of the current definitions and usages of the corresponding terms "autostylic," "hyostylic," "amphistylic" reveals considerable discrepancy, which is highly confusing to the general student; hence the present endeavor to standardize these terms and to give, as far as needed, their synonymy.

From the analysis necessary for the accomplishment of this purpose it has become evident that all the current definitions of "hyostylic," "autostylic" and "amphistylic" are in one way or other unsatisfactory, and that if these conceptions are to retain anything more than historic interest they will have to be extended to include the relations to the chondrocranium not only of the hyomandibular but also of the hyoidean arch as a whole and of its distal or ventral half, the "hyoid" or ceratohyal. By this extension we are enabled: first, to apply separate and clearly diagnostic terms to the suspensorial conditions of the very phylogenetically separated groups Dipnoi (autostylic) and Holocephali ("holostylic"), hitherto lumped together under the single term "autostylic"; second, to differentiate under the generic concept "hyostylic" four specifically well-marked modes, (a) the "hyostylic proper" of typical sharks, (b) the "amphystylic" of *Notidanus*, (c) the "euhyostylic" of most rays, (d) the "methyostylic" of the teleostomes; third to group all the modern types of suspensorial conditions under the term "cænostylic" in contrast with the ancestral type here called "palæostylic," which is only a few steps below Gadow's¹ suggested form, the "simple autostylic."

¹"On the Modifications of the First and Second Visceral Arches, etc.," *Philos. Trans.*, Vol. 179 (1888) B, p. 459.

TABLE A.

DESCRIPTIVE TERMS.								
SECOND VIS- CERAL ARCH.	HYOMANDIBULAR.	HYOID OR CERATOHYAL.	Huxley, '76.	Weider- sheim, '88. (Parker's.)	Zittel, 1902. (East- man's.)	Gadow, '88.	A. S. Wood- ward, '98.	Preferable Term.
PALATOQUADRATE.	HYOMANDIBULAR.	HYOID OR CERATOHYAL.						
Proximal or dorsal moiety of "first" visceral or oral arch.	Proximal or dorsal moiety of "second" visceral or hyoidean arch	Distal or v ntral moiety of "second" visceral arch.						Palæo- stylic.
Hypothetical Ancestor.	Not suspensorial	Not suspensorial.						
Preceded by "pre-oral" arches, gill bearing, not separated by distinct joint from distal (ventral) or mandibular portion. Slight or no cranial attachments. Loosely articulating with cranium. With postorbital process.	Very large; suspensorial; attached distally to jaws, pointing backward, movably articulating with cranium.	Retaining primitive connection with distal end of hyomandibular, closely applied to and supporting mandible.						Hyostylic.
<i>Chlamydoselachus.</i> (Fide Garman '85.) (Fig. 2.)	Of medium size; attached to cranium proximally by ligaments; of considerable suspensorial value; attached to junction of quadrate and mandible.	Articulating with distal end of hyomandibular, attached anteriorly to and supporting mandible.						Hyostylic.
<i>Cestracion.</i>	Closely articulating far forwards with cranium. Deep posteriorly.	Amphistylic. Low form of hyostylic.						Hyostylic.
<i>Notidanus.</i> (Fide Gadow '88.) (Fig. 4.)	Closely articulating with cranium, especially by "otic" process, much deepened posteriorly; inner joint with mandible incomplete. (Gadow.)	Retaining primitive connection with the distal end of the hyomandibular, attached by ligament to inner superior border of mandible; of slight or no suspensorial value.						Amphio- stylic.
Typica Sharks and <i>Squalina.</i> (Fig. 1.)	Loosely attached to cranium.	Retaining primitive connection with distal end of hyomandibular, attached anteriorly to and supporting mandible.						Hyostylic. <i>Sensen strictu.</i>

Typical Rays. (Fig. 3.)	Free from cranium.	Broken up.	Enlarged, the sole suspensorium.	Proximal end, partly by metapophy of hyo- mandibular, articulating in different forms at dif- ferent points along the hyomandibular, finally reaching the cranium, even gaining a distinct articulation with it; widely separated from the jaws; gill bearing. (Wiedersheim, Gadow.)	Hyostylic. Extreme form of hyostylic.	Hyostylic.	Hyostylic.	Hyostylic.	Euhyo- stylic.
<i>Polypterus</i> . (Fig. 6.)	Forming cartilaginous basis of palato-pterygo- quadrate series as in teleosts.	Broken up.	Large, with broad articulation with cran- ium in sphenoic re- gion, supporting oper- culum; buttressing metapterygoid and thus, indirectly, the quadrate. Capped by a pharyngohyal (?).	Modifying primitive connection with hyo- mandibular through in- tervention of the inter- or stylo-hyal; aiding in support of mandible.	Hyostylic.			Hyostylic	Methyo- stylic.
<i>Acipenser</i> .	Free from cranium.	Broken up.	Enlarged, the sole suspensorium through its separate symplec- tic segment.	Reduced, beginning the dorsal migration along the hyomandibu- lar towards the cranium. Modifying its hyo- mandibular connection by intervention of inter- hyal. Functioning chiefly in support of tongue and branchio- tegal bars.	Hyostylic.			Hyostylic.	Methyo- stylic.
'Typical teleosts. (Figs. 5, 7, 8.)	Forming cartilaginous basis of palato-pterygo- quadrate series.	Broken up.	Articulating with cranium in sphenoic region, distally sup- porting quadrate through the metapter- ygoid, symplectic and prooperculum; carry- ing the whole opercu- lar apparatus, which in turn braces the quadrate.	Hyostylic.	Hyostylic.			Hyostylic.	Methyo- stylic.
<i>Amphibia</i> . (<i>Fide</i> Gadow.) (Fig. 10.)	Partially fused with cranium, forming cartil- aginous basis of dermal bones.	Broken up.	Proximal part func- tioning as stapes (Gadow).	The proximal end having lost its connec- tion with the hyoman- dibular generally be- comes attached to the cranium as the stylo- hyal (Gadow).	Autostylic. Amphistylic (of larva).		Autostylic.		Auto- stylic.
<i>Ceratodus</i> . (<i>Fide</i> Huxley, '76, Gadow, '88.) (Fig. 9.)	Entirely fused with cranium, forming "sus- pensorial cartilage" posteriorly.	Broken up.	Reduced, united with cranium anteri- orly, bearing the oper- culum, conical distal portion, homologous with the symplectic (Huxley).	Connected by 'liga- ment with reduced hyo- mandibular.	Autostylic.		Autostylic.	{ Autostylic Holo- stylic.	Auto- stylic.
<i>Chimæra</i> . (See p. 61.) (Fig. 11.)	Entirely fused with cranium. Very short antero-posteriorly.	Intact.	Entirely separated from palato-quadrate and mandible, capped by small pharyngo- hyal.	Retaining primitive connection with hyo- mandibular.	Autostylic.		Autostylic.	{ Autostylic Holo- stylic.	Holo- stylic.

The foregoing table summarizes the relations in various forms of the first and second visceral arches to the chondrocranium, and gives the descriptive terms used by authors and the terms here adopted.

Upon this analysis the following definitions may be based.

PALÆOSTYLY: "First" visceral or mandibular and "second" visceral or hyoidean arches retaining in large part their primitive function as gill bearers, subequal in size, with slight or no connections with the chondrocranium; preoral gill arches. Hypothetical.

CÆNOSTYLY: "First" and "second" visceral arches modified in correlation with feeding, unequal in size, one or more of the elements attached to the cranium. Preoral arches changed in function (=labial cartilages and trabeculæ cranii.)

A. **HOLOSTYLY**¹: Palatoquadrate fused with chondrocranium; second visceral or hyoidean arch intact, non-suspensorial and free from the cranium. Holocephali.

B. **AUTOSTYLY**²: Palatoquadrate fused with chondrocranium; second visceral arch broken up and non-suspensorial, the hyomandibular reduced and united with the cranium. Dipnoi, Amphibia.

C. **HYOSTYLY**: Palatoquadrate articulating with chondrocranium, hyomandibular more or less suspensorial.

a. *Hyostyly proper*.³ Second visceral arch intact, the hyomandibular and hyoid segments forming a movable suspensorium for the upper and lower jaws. Most sharks, *Squatina*.

b. *Euhyostyly*.⁴ Second visceral arch broken up, the dorsal segment (hyomandibular) forming the sole suspensorium, the distal regment (ceratohyal) secondarily, free from all connection with the jaws, functioning solely as a gill bearer. Most rays.

¹ "Holo," in allusion, either to "Holocephali," or to the fact that probably since early Palæozoic times the palatoquadrate and the cranium have formed a continuous whole.

² The term "autostylic," hitherto applied to both Dipnoi and Holocephali is here restricted to apply only to the former.

³ "Hyostyly proper" because the ordinary sharks furnish the traditional type of this condition.

⁴ "Euhyostyly," as a progression upon or development of the "hyostyly proper."

*c. Amphystyly.*¹ Second visceral arch intact, of slight suspensorial value, much smaller than first arch; palatoquadrate deep posteriorly, articulating by its "otic process" with the chondrocranium. *Notidanus*, *Pleuracanthus*.

*d. Methystyly.*² Second visceral arch broken up (*i. e.*, with the component segments more or less shifted out of their primitive sequence or relations); symplectic, metapterygoid, pre- and interopercular when present assisting the hyomandibular in the support or bracing of the quadrate and mandible.

The value and permanence of this classification will depend on whether the hyomandibular of teleostomes is homologous, as generally supposed, with that of elasmobranchs. This has been called into question by Pollard ('94) but as his conclusions have not been adopted by subsequent authorities it seems best to accept the traditional view that these elements are truly homologous in the two groups.

The application of these terms in classification and phylogeny is illustrated in the diagram on page 60.

PREVIOUS DEFINITIONS.

Huxley. — The terms "autostylic," "amphistylic," "hyostylic" were first used by Huxley in his paper of 1876 on *Ceratodus*.³ The passage in which "autostylic" is defined is as follows (*op. cit.*, p. 40):

"The part of the palato-quadrate cartilage [of *Ceratodus*] which is united with the skull, between the exits of the fifth and second nerves, answers to the "pedicle of the suspensorium" of the amphibian, while its backward and upward continuation onto the periotic cartilage corresponds with the otic process. As in the Amphibia and in the higher Vertebrata, the mandibular arch is thus attached directly to the skull by that part of

¹ "Amphystyly"; this term retains the element "amphi," so long used (in *amphistylic*) of these forms, while clearly indicating its subordination under hyostyly.

² "Methystyly," in allusion either to the prominence of the metapterygoid in the suspensorium, or to the fact that methystyly represents a morphological advance upon earlier modes.

³ *Proc. Zool. Soc. Lond.*, 1876, pp. 24-59. "The Scientific Memoirs of Thomas Henry Huxley," Vol. IV., 1902, pp. 84-127.

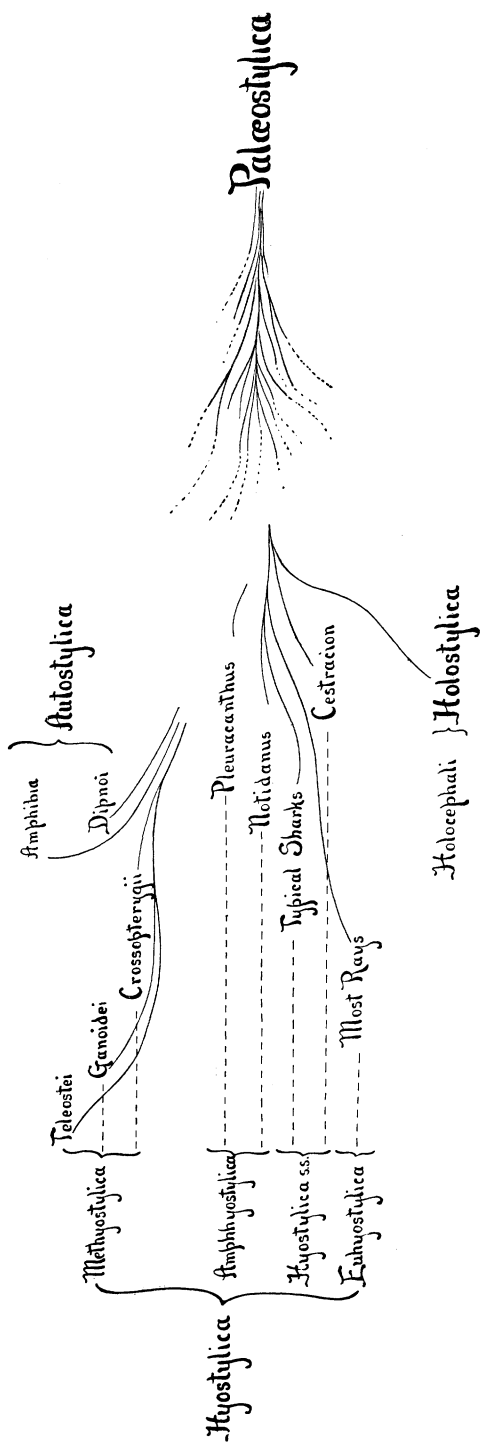


FIG. 1. Application of the newly defined terms to the phylogeny of the fishes.

its own substance which constitutes the suspensorium. It may thus be said to be *autostylic*.

"Among fishes the only [other ?] groups which possess an autostylic skull or in which the dorsal end of the mandibular arch is continuous with the cartilage of the brain case are the Chimæroids and the Marsipobranchii."

In this definition of autostyly attention is centered solely upon the relations of the *first* arch with the skull. Huxley notes that in the autostylic *Ceratodus* the hyomandibular is reduced and fused with the skull, but he also uses "autostylic" for *Chimæra* in which the hyomandibular is separate (see above, Table A). For comparison with "hyostylic" and "amphistylic" we may summarize Huxley's description as follows :

AUTOSTYLIC SKULL : *Mandibular or first visceral arch attached to the skull solely by its own dorsal moiety, the palatoquadrate, which is continuous with the skull.*

Huxley describes the HYOSTYLIC and AMPHISTYLIC conditions as follows (p. 41) :

"In all other Fishes, except the Marsipobranchii, the mode of connection of the mandibular arch with the skull is different from that which obtains in the Chimæroids and the Dipnoi. The palatoquadrate cartilage is no longer continuous with the chondrocranium . . . but is, at most, united with it by ligament. Moreover the dorsal element of the hyoidean arch, or the hyomandibular, usually attains a large size and becomes the chief apparatus of suspension of the hinder end of the palatoquadrate cartilage with the skull. Skulls formed upon this type, which is exemplified in perfection in Ganoidei, Teleostei, and ordinary Plagiostomes, may therefore be termed *hyostylic*.

"But though the typical forms of autostylic and hyostylic skulls, as exemplified, *e. g.*, by a Sturgeon, a Pike, and a Dogfish or Ray, on the one hand, and *Chimæra*, *Ceratodus*, and *Menobranchius* on the other, are thus widely different, certain Plagiostomes present a condition of the cranium which tends to connect the two by a middle form, which may be termed *amphistylic*."

"In the amphistylic skull the palato-quadrate cartilage is quite distinct from the rest of the skull ; but it is wholly, or almost wholly, suspended by its own ligaments, the hyomandibular being small and contributing but little to its support. The embryo amphibian is amphistylic before it becomes autostylic ; and, in view of certain palæontological facts, it is very interesting that the link which connects the amphistylic with the ordinary Selachian skull is that of *Cestracion*."

Huxley's conception of hyostyly and amphistyly may be restated as follows :

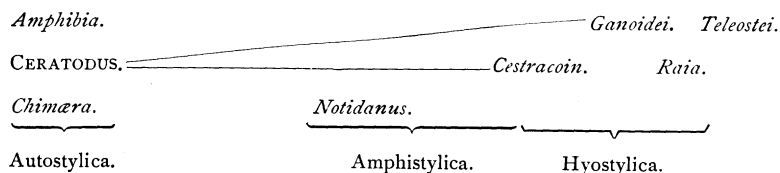
HYOSTYLIC SKULL: *Mandibular or first visceral arch not continuous with the skull in its dorsal portion (the palatoquadrate); the hinder end of the palatoquadrate is chiefly connected with the chondrocranium by means of the hyomandibular or dorsal portion of the hyoidean arch.*

AMPHISTYLIC SKULL: *Mandibular, or first visceral arch attached to the skull wholly or almost wholly by means of its dorsal portion the palatoquadrate, not however by fusion or continuity, but by ligaments; the hyoidean arch contributes but little to its support.*

The Huxleyan conception of amphistily is that it is in some respects a "middle form," resembling autostily in the suspensorial self-sufficiency of the first visceral arch, but resembling hyostily in the lack of confluence of the palatoquadrate with the skull. A similar use of the prefix "amphi" occurs in "*Amphitherium*," which genus was at first supposed to combine mammalian and reptilian characters.

The element "stylic" from *στῦλος*, a pillar, evidently refers to the quadrate region in its architectural relation to the skull. The skull of *Chimæra* seems to have been regarded by Huxley as primitive (so far as I can determine from a careful study of the entire article) and hence in an autostylic skull the palatoquadrate must have been conceived as belonging to the skull: therefore the forces acting upon the jaws in eating would be transmitted to the skull chiefly through the quadrate, *its own pillar* (hence auto, stylic), whereas in the typical hyostylic skull these forces would be transmitted chiefly through the pillar of the hyoidean arch (the hyomandibular) — hence "hyostylic."

Huxley's conception of the phylogenetic relations of the three types of cranial structure are expressed in the following diagram (*op. cit.*, p. 45):



The left-hand column (autostylia) includes the (to Huxley) more generalized types, the most primitive, *Chimæra*, standing at

the bottom of the column ; progressive stages of skull structure are represented in the middle and right-hand columns. The cranial plan of *Ceratodus* is regarded as representing the ancestral condition of both *Cestracion* and the Ganoids. *Cestracion*, classed with *Notidanus* as an amphistylitic type, is regarded also as transitional, a low form of the hyostylic type.¹ The diagram confirms the inference that Huxley conceived the palatoquadrate as originally a part of the skull, which gradually became constricted off as in *Ceratodus* and finally freed from it entirely as in *Raia* and the Teleosts.

Wiedersheim (*Parker's translation*, '97). —

"The palatoquadrate is usually only united to the basis cranii by ligaments, but in the Chimæroids. . . it becomes immovably fused with it, whence their name of Holocephali. In the Sharks and Rays the palatoquadrate is not directly united to the skull, but is suspended from it by the *hyomandibular*. . . . In this case the skull may be described as *hyostylic*, to distinguish it from *autostylic* skulls, in which the hyoid takes no part in the suspensorium" (*op. cit.*, p. 75).

Comments : (1) "Hyoid" here refers to the hyoidean arch, not to the hyoid or ceratohyal. (2) In general it would be less confusing to say that it is the *mandible* rather than the palatoquadrate which is suspended from the hyomandibular, and that the palatoquadrate rests chiefly upon and is fastened to the mandible.

v. Zittel, 1903 (*Eastman's edition*). —

"In the Holocephali the palatoquadrate and hyomandibular fuse together and with the cranial capsule. The mandible thus becomes autostylic, *i. e.*, articulates directly with the cranium" (*op. cit.*, p. 11).

Comments : (1) The statement in regard to the hyomandibular seems incorrect. In a specimen of *Chimæra collei* kindly loaned to me by Professor Bashford Dean the hyomandibular is seen to be a large independent element (see Fig. 11) serially homologous with the epibranchials as in Selachii, and tipped with a reduced pharyngohyal, both being free from the chondrocranium. (2) To apply the term autostylic to the *mandible* is to introduce a new element of confusion in a matter already sufficiently complicated.

¹ On page 43 of Huxley's memoir the *Cestracion* skull is referred to as a low form of "autostylic type," but examination of the context and of the diagram cited show that this is probably a misprint for "hyostylic."

Parker and Haswell (1897). —

"In some fishes the hyomandibular articulates above with the auditory region of the cranium while the jaws are connected with its ventral end. We may thus distinguish two kinds of *suspensorium* or jaw-suspending apparatus, a *mandibular suspensorium*, furnished by the quadrate, and a *hyoidean suspensorium* by the hyomandibular; in the former case the skull is said to be *autostylic*, *i. e.*, having the jaw connected by means of its own arch, in the latter it is called *hyostylic*; in a few cases an *amphistylic* arrangement is produced by the articulation of both mandibular and hyoid arches with the skull" (*op. cit.*, p. 71).

On page 161 we read that in *Hexanchus* and *Heptanchus*: ". . . there is a prominent post-orbital process of the palatoquadrate for articulation with the post-orbital region of the skull (amphistylic arrangement)."

The definitions cited may be criticised on several grounds:

1. There are several ambiguities latent in these sentences which experience proves to be exceedingly puzzling to the student: (a) "jaw" and "jaws" thus used require the most careful analysis to determine which jaws, upper or lower, are intended; (b) a *mandibular suspensorium* is no doubt equivalent to "a suspensorium furnished by the mandibular or first visceral arch"¹ but if "mandibular" be mistakenly interpreted as referring to the mandible the very pith of the definition is lost; (c) *suspensorium* or jaw-suspending apparatus is understood first with reference to the lower jaw, then to the upper; (d) "hyoid" arch is used on this same page (71) as referring to the whole second visceral arch, but on page 161 "hyoid arch" is used of the ceratohyal or hyoid only.

2. The definition of autostylic does not exclude *Notidanus* (which Parker and Haswell themselves call "amphistylic") because in it the hyomandibular takes so small a share in suspension that the suspensorium may be said to be "furnished by the quadrate."

3. The definition of amphistylic as implying the articulation of "both mandibular and hyoid arches with the skull" is exceedingly imperfect. As shown above (Table A, pp. 54, 55) the articulation of both mandibular and hyoidean arches with the skull is not diagnostic of amphistily since on the one hand both arches

¹ Especially since "mandibular" is used in that sense at the top of the same page.

articulate with the skull in many hyostylic types, and on the other hand in the amphistylic *Notidanus* both arches do not articulate with the skull since the hyomandibular is connected with it only through ligaments (Gadow, '88, Pl. 71, Fig. 1, A).

Gadow (1888). —

Gadow apparently uses the terms in their etymological significance, rather than with the limitations imposed by established usage. Thus he speaks (p. 455) of the "autostylic condition of the *Notidanidæ*" (the "amphistylic" of authors) and applies the same term to the Amphibia (p. 481) and the Dipnoi (p. 459), evidently having in mind the self-sufficiency in all these cases of the first arch as its own suspensorium; so too, "simple autostylic" (p. 459) apparently refers to the ancient and generalized condition from which the modern modes have been derived (cf. "palæostylic," proposed above) and in which the oral arch had not yet begun to borrow support from the hyoidean arch. Again Gadow applies "holostylic" (p. 458) to *Chimæra*, *Ceratodus* and *Cestracion* evidently with reference to the functional ligamentous union of the upper jaw with the cranium in *Cestracion* and to its fusion therewith in *Chimæra* and *Ceratodus*. "Amphistylic" in its etymological sense serves to describe the conditions in "most selachians" (p. 481), in which *both* oral and hyoidean arches are suspensorial, while etymologically the rays are pre-eminently "hyostylic" (p. 481) since the dorsal element of the *hyoidean* arch, the hyomandibular, is the sole suspensorium (cf. our "euhyostylic," p. 56, *supra*).

But while this bold and highly suggestive use of terms has finally bred in me several clarifying ideas I cannot deny that formerly, wishing to refer to isolated passages of Gadow's work, I experienced a most baffling uncertainty as to his meaning.

Smith Woodward (1897). —

"Among the fishes existing at the present day there may be observed two distinct plans of cranial structure, between which no definitely intermediate conditions can be recognized. In *Chimæra*, *Protopterus*, *Ceratodus* and their allies, the upper segment of the mandibular arch is directly fused with the chondrocranium, while the corresponding segment of the hyoid arch is atrophied or absent; in the Elasmobranchs and the so-called "Ganoidei" and "Teleostei" the same elements are loosely articulated with the chondrocranium, the upper segment of the hyoid arch forming a

movable suspensorium. The first condition is now commonly known as the *autostylic*, and the second as the *hyostylic*."

Comments. — This passage is perfectly clear and illuminating. It adheres closely to the essential features of Huxley's conceptions, and it makes a decided advance beyond them not only in stating clearly that between modern autostyly and hyostyly "no definitely intermediate conditions can be recognized," but also in implicitly reducing the amphistylic mode to its true place as a special phase of the hyostylic — a suggestion which has been followed in the present paper (see above, pp. 57, 59).

But not even these definitions, I think, will survive. They fail to emphasize the differences between the autostyly of Dipnoi and the autostyly (here termed "holostyly") of Chimæroids; nor do they indicate that by taking also the distal segment of the hyoidean arch into account we may place the whole subject upon a new, and apparently phylogenetic basis.

In conclusion I desire to thank Professor Henry Fairfield Osborn and especially Professor Bashford Dean for various courtesies and suggestions.

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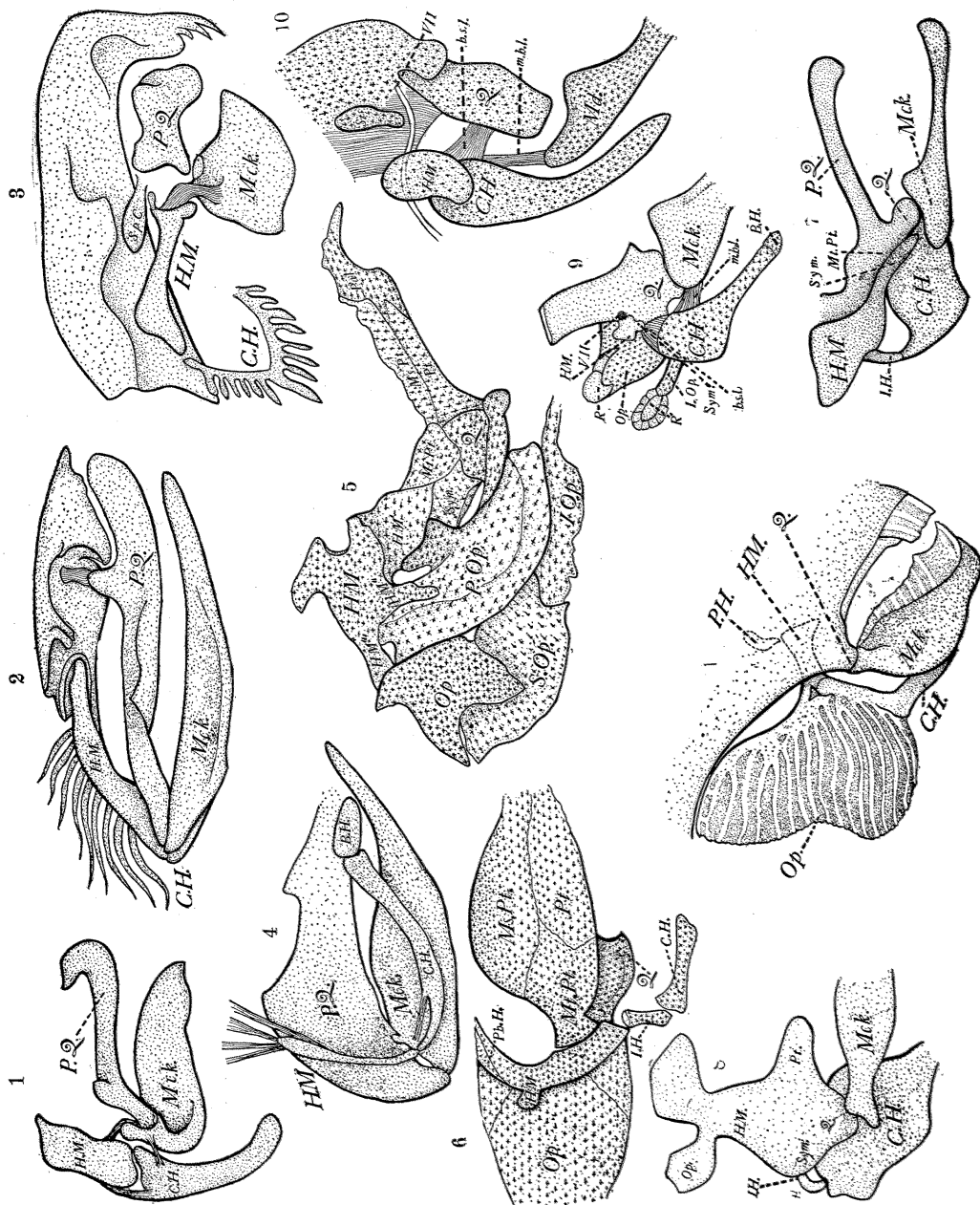
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February 10, 1904.

PLATE I.

EXPLANATION OF ABBREVIATIONS.

<i>P. Q.</i> , Palatoquadrate.	<i>H. M''</i> ., Median limb of ditto.
<i>Mck.</i> , Mandible (Meckelian cartilage).	<i>H. M'''</i> ., Posterior limb of ditto.
<i>H. M.</i> , Hyomandibular (epihyal).	<i>Sym.</i> , Symplectic.
<i>B. H.</i> , Basihyal.	<i>Q.</i> , Quadrate.
<i>C. H.</i> , Ceratohyal.	<i>P. Op.</i> , Preoperculum.
<i>P. H.</i> , Pharyngohyal.	<i>I. Op.</i> , Interoperculum.
<i>Sp. C.</i> , Spiracular cartilage.	<i>Op.</i> , Operculum.
<i>I. H.</i> , Inter- or stylohyal.	<i>S. Op.</i> , Suboperculum.
<i>Pal.</i> , Palatine.	<i>VII.</i> , Aperture for seventh nerve.
<i>Ms. Pt.</i> , Mesopterygoid (entopterygoid).	<i>h. s. l.</i> , Hyosuspensorial ligament.
<i>Pt.</i> , Pterygoid.	<i>m. h. l.</i> , Mandibulohyoid ligament.
<i>Mt. Pt.</i> , Metapterygoid.	<i>St.</i> , Stapes.
<i>H. M'.</i> , Anterior limb of hyomandibular.	

Cartilaginous elements stippled, osseous elements with small crosses.

FIG. 1. "Hyostyly proper." *Centrophorus granulosus*. Embryo. After Gadow.

FIG. 2. "Hyostyly proper." *Chlamydoselachus anguineus*. After Garman.

FIG. 3. "Euhyostyly." *Trygon* sp. After Gadow.

FIG. 4. "Amphyostyly." *Heptanchus cinereus*. Internal view. After Gadow.

FIG. 5. "Methyostyly." Diagram of the relations of the suspensorial and opercular regions in the cod.

FIG. 6. Methyostyly. *Polypterus*. View from within and below. The metapterygoid is supported by the hyomandibular.

FIG. 7. Cartilaginous basis of methyostylic arrangement in the young salmon. After Parker and Bettany.

FIG. 8. Cartilaginous basis of methyostylic arrangement in a larval siluroid. After Pollard. All the cartilages of the suspensorial region seem to have secondarily coalesced.

FIG. 9. "Autostyly." *Ceratodus*. After Huxley. *R*, *R'*, vestigial hyoid rays. The operculum is borne by the reduced hyomandibular.

FIG. 10. "Autostyly." *Proteus*. After Gadow. The stapes represents the upper portion of the hyomandibular (Gadow).

FIG. 11. "Holostyly" *Chimæra collei*.